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A Vicariance Approach to Historical Biogeography

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Historical biogeography is a peculiar discipline because most of its practitioners are not biogeographers per se but systematists specializing on some group of organisms. Systematists know that their task is studying the distribution of characters among various species to discover how the species are interrelated, what groups of them (taxa) exist, and what their origins may be. But what is the task of biogeographers? One could say that biogeographers study the distribution of species among various areas of the world to discover how the areas are interrelated, what groups of them (regions) exist, and what their origins may be. But what are biogeographic regions, and how can they be recognized? In what sense are they "related" to each other, and what is the pattern of their interrelationship? What has caused the pattern?

THE PAST: DISPERSAL AND VICARIANCE

One of the earliest attempts to interpret the distribution of organisms was that of Linnaeus, who believed that the earth's landmass is growing in size. He concluded that, if this growth process had operated in the past, "the Continent in the first ages of the world lay immersed under the sea, except a single island in the midst of this immense ocean; where all animals lived commodiously, and all vegetables were produced in the greatest luxuriance" (Linnaeus 1781, p. 77). Recognizing that organisms differ in their climatic requirements, Linnaeus proposed that the primordial island was situated in the tropics and bore "a very lofty mountain," which was inhabited at various altitudes by species with different ecologies. As the sea receded and new land emerged, Linnaeus conjectured, organisms migrated by active and passive means to colonize all the areas that met their ecological requirements, and these are where they occur today.

Quaint as these ideas may seem, they contained the basic premise—a small area (or center) in which species originate and from which they disperse—of a "center of origin/dispersal explanation," which was frequently advanced during the subsequent two centuries. Like all center of origin/dispersal explanations, Linnaeus' hypothesis is difficult to test; it seems to allow any number of species to occur anywhere and to be interrelated (grouped together in higher taxa) in any way. If he was correct, different parts of the world—to the extent that they have the same physical conditions—should house the same species.

This expectation was quickly contradicted by Linnaeus' contemporaries. When Buffon (1761), for example, studied the mammals then known from tropical Africa and America, he discovered that no single species occurred on both continents. Other workers soon confirmed that the same anomaly was true for other groups of organisms, and "Buffon's law"—that different areas have different species even if they have similar ecologies—became generalized to include virtually all animals and plants (Nelson 1978).

Information on Buffon's law of endemism accumulated so rapidly that, by 1820, the French botanist Candolle was able to supply a list of at least 20 botanical regions containing plants unique to themselves:

> Botanists know that in general the plants from these twenty regions are different, the ones from the others, such that when one finds in the writing of an explorer that the plants of one of these regions have been found in another, one must, before supposing such to be true, study the specimens from the two areas with particular care. (Candolle 1820, p. 412)

Candolle also reasoned that, since ecological similarities alone cannot account for these regions, they "are probably determined in part by geological causes that no longer exist today" (1820, p. 413).

Candolle's views were adopted by the English botanist Joseph Hooker, who studied the floras of the south temperate parts of the world and concluded not only that there are distinctive floras in South Africa, Australia, and southern South America, but also that

> many of the peculiarities of each of the three great areas of land in the southern latitudes are representative ones, effecting a botanical relationship as strong as that which prevails throughout the lands within the Arctic and Northern Temperate zones, and which is not to be accounted for by any theory of transport or variation, but which is agreeable to the hypothesis of all being members of a once more extensive flora, which has been broken up by geological and climatic causes (Hooker 1853, p. xxxvi).

Hooker reasoned further that because the various southern floras are more closely related to each other than to the floras of the northern continents, the divergence of the northern and southern floras must have antedated the breakup of the "once more extensive flora," which he thought must have existed in the south. Hooker's views are an early example of a type of "vicariance explanation" in which Buffon's law is attributed not to dispersal across barriers, but to the appearance of barriers dividing

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formerly continuous habitats and species ranges.

Fellow countryman A. R. Wallace, however, did not accept Hooker's imaginative suggestion of the existence of former land connections among the various southern continents and islands. He suggested an alternative explanation:

> The north and south division truly represents the fact, that the great northern continents are the seat and birth-place of all the higher forms of life, while the southern continents have derived the greater part, if not the whole, of their vertebrate fauna from the north; but it implies the erroneous conclusion, that the chief southern lands—Australia and South America—are more closely related to each other than to the northern continent. The fact, however, is that the fauna of each has been derived, independently, and perhaps at very different times, from the north, with which they therefore have a true genetic relation; while any intercommunion between themselves has been comparatively recent and superficial, and has in no way modified the great features of animal life in each. . . . We have the strongest proof that South America was peopled from the Nearctic, and Australia and Africa from the Palaearctic region; hence, the Eastern and Western Hemispheres are the two great branches of the tree of life of our globe. (Wallace 1876, 2:159)

Thus, Wallace believed that faunas do have relationships, that is, that biogeographic relationships really exist. He evidently considered the relationships to be specifiable, so that we might say that the South American fauna is more closely related to the North American one than to the Australian one. Wallace also thought that the relationships were true not merely for one group of organisms or another but for "the tree of life" in general. Moreover, to Wallace the nature of biogeographic relationships was genetic—that is, caused by the phylogenetic history of organisms, such as by lineages originating in the north and invading the south. Finally, for Wallace biogeographic relationships were relatively unproblematical; he did not hesitate to speak of "true genetic relationships" or to claim that he had the "strongest proof" of them.

It's not surprising that Wallace held the views he did, for he was writing in colonial times when the "higher forms of life" (the "Favoured Races" of the full title of Darwin's *On the Origin of Species*) inhabiting the northern continents were busy invading and dominating the less favored areas and races of the south. But his view of distribution as being due to dispersal from the north on an earth largely stable in its major geographical features quickly became established as orthodox. In fact, it remained entrenched until the plate tectonics revolution in geology in the 1960s made it impossible to regard the earth as largely stable.

With the revival of theories of continental drift, the biogeographic tradition associated with Wallace and Darwin seemed likely to have been based on some fundamental error. No longer could biogeographers reconstruct a phylogenetic tree for some group of organisms, lay it on a map, and then simply read out the dispersal routes taken by the group during its history, as done, for example, by Darlington (1959). We can still agree with Wallace that biogeographic relationships exist, are specifiable, might be general, and reflect phylogenetic history. But are they unproblematical?

BIOGEOGRAPHIC RELATIONSHIPS

Both center of origin/dispersal and vicariance hypotheses are causal explanations of a pattern of biogeographic relationship and, therefore, presuppose that such patterns are identifiable. But what does it mean to say that areas, or their biotas, are related? We might pick any two species and say that they are related; for example, a flatworm and a bat are related because they are both metazoans. We could also pick any two areas of the world containing endemic species, such as the Galapagos Islands and the Himalayan Mountains, and say that they, too, are related, even if only at the level of sharing some groups of metazoan animals. But in both cases, we need three subjects before we can make a comparative statement of relationships (e.g., that A and B are more closely related to each other than either of them is to C). Let us, therefore, take three obvious areas of endemism—Java, Borneo, and Sumatra—and ask how they are interrelated.

As long ago as 1863, Wallace explored the faunas of these islands and the Asian mainland and concluded that Sumatra and the mainland were "the most recently dismembered" areas, followed by Borneo and, still earlier, by Java. Without the mainland, Wallace's views of the interrelationships of the islands can be represented by a cladogram (Figure 1.1). His conclusions were based on the relative numbers of endemic taxa in the areas: "Java, in fact, possesses more birds and insects peculiar to itself than either Sumatra or Borneo, and this would indicate that it was earliest separated from the continent" (Wallace 1863, p. 228). If further investigation revealed additional endemic taxa on Sumatra or Borneo, however, Wallace's concept would not necessarily be wrong. The newly discovered species would merely confirm that Sumatra and Borneo are indeed areas of endemism. Hence, the only conclusion that can be drawn from data like Wallace's on the numbers of endemic taxa is that there are areas of endemism (Figure 1.2).

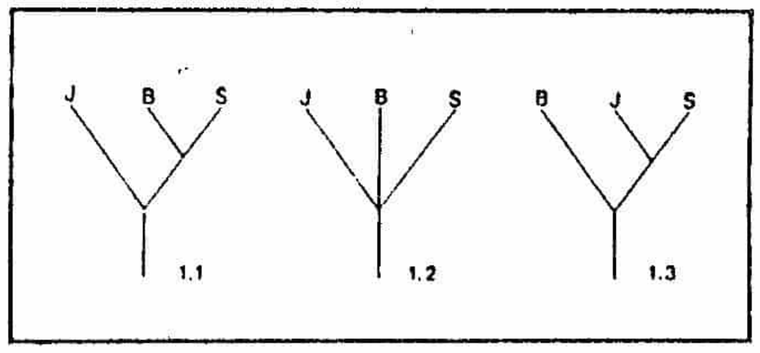

Figure 1. Area cladograms for Java (J), Borneo (B), and Sumatra (S); those areas connected at the uppermost nodes are the most closely related. 1.1: Adapted from Wallace (1863). 1.2: Supported by data from Wallace (1863) and Darlington (1957). 1.3: Adapted from Darlington (1957).

Nearly a century later, Darlington (1957) reexamined the biota of the three islands and stated that "Java shares more fresh-water fishes with Sumatra than with Borneo, as if exchange between Java and Borneo was interrupted earlier" (p. 489). He did not provide counts of the number of fish species shared by the islands, but his argument was that if we find that Java shares 400 species with Sumatra but only 100 with Borneo, and that Borneo and Sumatra share only 100 species with each other, we can conclude that the biotas of Java and Sumatra are more closely related to each other than either is to that of Borneo (Figure 1.3). But if further investigation revealed additional species shared by Java and Borneo, Darlington's concept would not necessarily be wrong. The only conclusion that can be drawn from data like his on the numbers of shared taxa is again uninformative (Figure 1.2).

Why is this the case? If we assume that

- the three islands were once connected parts of a single landmass (in fact, geological evidence indicates that they were connected to each other and to the mainland until relatively recently);
- Darlington's idea of the history of the region (Figure 1.3) is correct, and Bor-

neo was disconnected from the other areas before Java and Sumatra were separated from each other; and

• prior to the two disconnections, a single species occurred over the entire, unseparated landmass (Figure 2.1);

then what would happen when the first event—separating Borneo from the other areas—occurred? Speciation could occur, resulting in a pair of sister species, one on Borneo and the other on Java plus Sumatra (Figure 2.2). Or speciation might not occur, if the new barrier separating Borneo from the other two areas does not affect the species because of the organism's particular capabilities for dispersing across it. A barrier that is effective in isolating populations of flies, for example, may not also isolate populations of birds.

Then what will happen when the second disconnection occurs, and a new barrier appears between Java and Sumatra? If the dispersion capabilities of the organisms allow them to cross the new barrier as part of their normal activity ranges, nothing will happen. Indeed, for speciation to occur through isolation, either Java or Sumatra must be effectively isolated by the new event not only from Borneo but from each other as well; a barrier between just Java and Sumatra is not sufficient to isolate the two areas (Figure 2.3). If the population on Java did become effectively isolated from that on Sumatra, but still retained its dispersion contacts with Borneo, then a species endemic to Sumatra could have its closest relative occurring on both Java and Borneo (Figure 2.4). Similarly, if the new barrier between Java and Sumatra effectively isolated Java and Borneo as well, a species endemic to Java could have its closest relative occurring on both Sumatra and Borneo (Figure 2.5). Thus, the same two historical events—separating first Borneo and then Java from Sumatra—could produce species shared by any pair of the islands. Finding a species that is shared by two islands tells us nothing about the sequence of disconnections, because it could be the result of a more recent historical relationship between any pair of the areas. Shared (widespread) taxa, such as Darlington's fishes, contribute no unambiguous information about area interrelationships.

To investigate questions about area relationships, then, we must have not only data on the numbers of endemic or shared taxa, but also data on the interrelationships of groups that have endemic representatives in the areas under study. A group of three related fish species, each of which is restricted to one island and for which a hypothesis of relationships (like Figure 1.1) can be constructed, will supply an unambiguous hypothesis of area interrelationships. We can test for generality by investigating other groups of organisms with similarly distributed species to see if they are similarly interrelated (Platnick and Nelson 1978). Indeed, groups with three or more species of which some are widespread, or in which more than one species occurs in a given area, can also contribute useful (if somewhat more ambiguous) information (Nelson and Platnick 1980).

If Buffon's law of endemism is correct, what are the areas of endemism, and how many exist in the world? No one knows. Some may be relatively small:

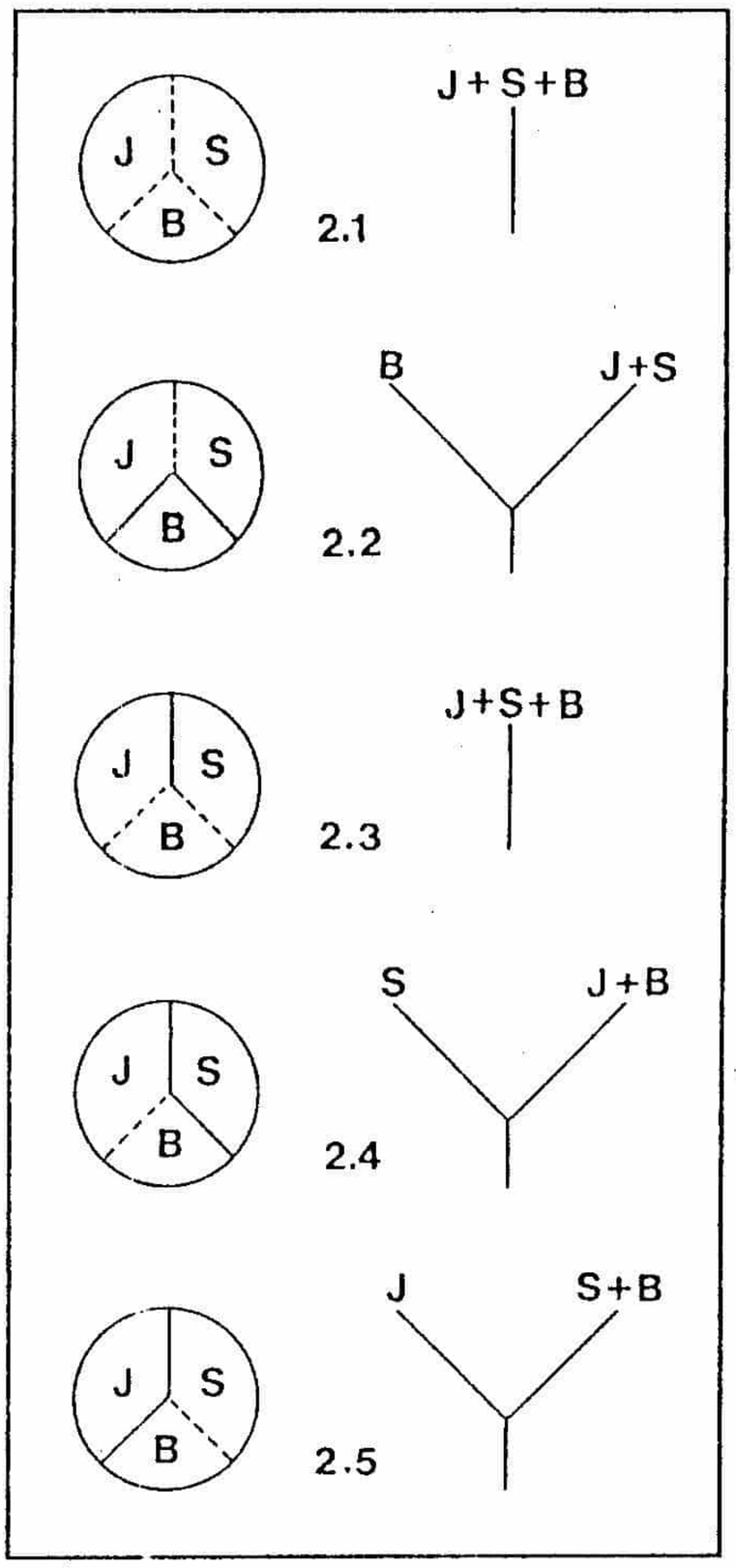

Figure 2. Generalized maps of a united Java (J), Borneo (B), and Sumatra (S), showing possible barriers (left), and the species cladograms resulting from the possible effects of the barriers on a species occupying the united area (right). 2.1: No barriers. 2.2: Barrier isolating Borneo. 2.3: Barrier separating Java and Sumatra. 2.4: Barrier separating Java and Sumatra and isolating Sumatra. 2.5: Barrier separating Java and Sumatra and isolating Java.

There are groups of millipedes and of carabid beetles, for example, that have many species in the southeastern United States, some of which are restricted to a single county or mountaintop. But no one has determined whether the areas that house endemic millipedes also house endemic carabids or endemic species of other groups of organisms. On a larger scale, however, there are clearly many areas of endemism, be they islands like Java, mountains like the Himalayas, or deserts like the Namib.

Is there, then, a general set of interrelationships that might be true for all groups of organisms containing taxa endemic to the areas, or for more such groups than could be expected by chance alone? Here again, no one knows. A provisional answer was given by Leon Croizat (see the references in Nelson 1973), who examined the distributions of thousands of groups of plants and animals and discovered that plotting the ranges of related taxa on a map and connecting them with a line or track revealed not a random assortment of tracks around the globe but a relatively small number of generalized tracks into which the distributions of many different groups of organisms fit. Observing that the tracks did not, in general, correspond to present-day geography, Croizat concluded that, although the "map of this day keeps the records [of distribution,] the maps of the past rationally account for them" (Croizat 1964, p. 85). If there are general patterns of area interrelationships, how can they be explained by events of the past?

AREA CLADOGRAMS

"Hooker and Wallace, as you recall, each supplied an explanation for the origin of the endemic biotas of the south temperate continents and islands that referred to past events (dispersals from the north, for Wallace, and the breakup of a formerly continuous southern biota, for Hooker). Which view is correct? If we favor Hooker, areas of endemism in the south should be most closely related to each other; if Wallace is correct, they should be most closely related not to each other but to areas of endemism in the north. To decide, we must find groups with representatives in both the northern and southern regions of the world, which are subdivided such that they have endemic representatives in at least one northern and two separate southern areas.

Groups meeting these requirements were studied by Lars Brundin, a special-

ist on Diptera, in 1966. Brundin devoted most of his attention to the Podonominae and Diamesinae, two subfamilies of chironomid midges that are relatively speciose (containing about 150 and 110 species, respectively) and that have markedly bipolar distributions, with representatives in South Africa, Australia, New Zealand, temperate South America, and in the northern parts of North America and Eurasia—and without members in the intervening tropical lowlands. Fortunately, chironomids are especially well suited to studies of interrelationships. Each of three life stages (larvae, pupae, and adults) provides a source of numerous complex taxonomic characters, and the species cladograms suggested by the features of one stage can be tested against the characters of the other two stages (see Platnick and Nelson 1980 for an introduction to species cladograms and their use in taxonomy).

In the Podonominae, Brundin found seven species or pairs of sister species endemic to Australia. If Wallace was correct, their closest relatives should be to the north, in eastern Asia. But Brundin's research indicated that each of the Australian endemics has its closest relatives in South America, and only much more distant relatives in northern areas. Moreover, the one group of endemic Australian Diamesinae had its closest relatives in South America, and, in the related subfamily Aphroteniinae, the two known groups of Australian endemics again had South American taxa as the nearest relatives. In all three subfamilies, then, Brundin found that Australian and South American taxa are more closely related to each other than they are to African endemics (Figure 3.1), which corroborates Hooker's hypothesis.

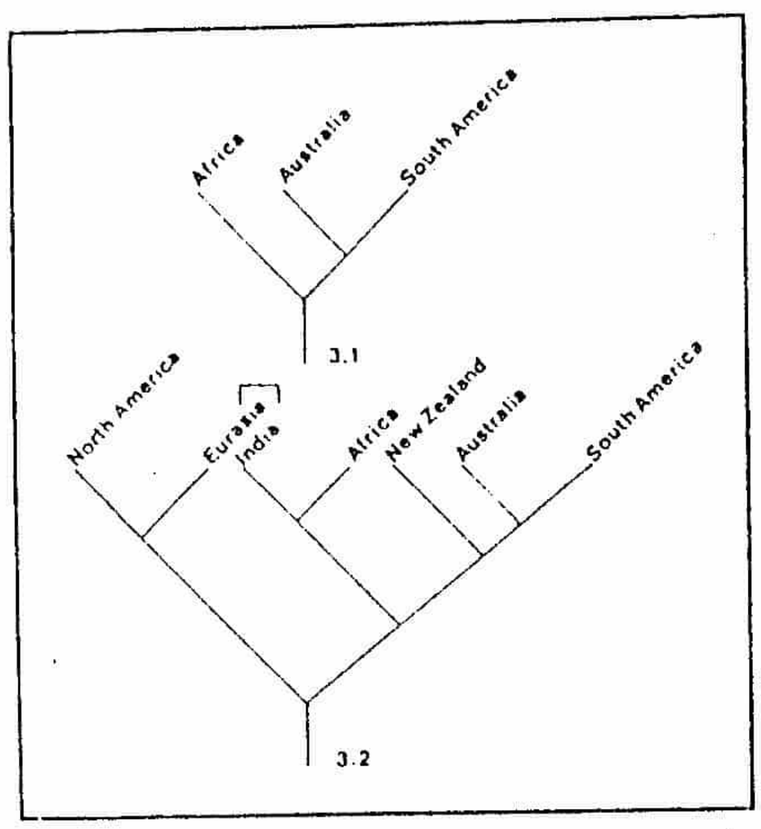

Figure 3. Area cladograms for major continental blocks. 3.1: Biological area cladogram, adapted from Brundin (1966). 3.2: Geological area cladogram, adapted from Rosen (1978).

Does this pattern correlate with the actual history of the areas? The usual view of plate tectonics covers Brundin's case, with the Pangaean supercontinent splitting into a northern Laurasia (now North America and Eurasia except for India) and a southern Gondwanaland (now Australia, New Zealand, South America, Africa, India, and perhaps other areas). Both Laurasia and Gondwanaland have undergone subsequent fragmentation, and India has been sutured onto mainland Asia. These conventional views of continental drift can be summarized in a geological area cladogram (Figure 3.2).

If we abstract from this geological area cladogram a simpler statement concerning only the three areas—Africa, Australia, and South America—for which we have a biological area cladogram (based on Brundin's midge groups), we find that the two area cladograms are identical (Figure 3.1). Hence, the fragmentation of Gondwanaland seems to be the best available estimate of the cause of the biological area cladogram. The age of the disjunctions of the midge groups, then, can be inferred to be about 70 million years for the separation of their Australian and South American components and about 85 million years for the earlier separation of their African components.

Could the cladogram be true for *all* groups with endemic representatives in Australia, South America, and Africa? There is no shortage of groups with such distributions, but there are few explicit hypotheses of the interrelationships of their endemic members in the literature. According to Rosen (1978), however, the pattern found in Brundin's midge groups is also true for salmoniform fishes of the subfamily Galaxiinae.

Biologists, then, must produce detailed studies of the interrelationships of endemic taxa of various groups of organisms, summarize these studies in species cladograms based on the distributions of features unique to different sets of the species, and compare species cladograms of various organisms in search of general patterns of geographic relationship that can be summarized in biological area cladograms. Geologists, for their part, need to relate now disjunct areas on the basis of unique features of paleomagnetism, stratigraphy, etc., and present their results in the form of a geological area cladogram that can be compared to a biological one for the same areas.

Both types of studies, biological and geological, can thus be used to produce classifications of areas. The question remains, of course, as to whether the results of either type of study represent the true history of areas and their biotas (i.e., whether the classifications they produce are natural ones). In systematics, a similar question arises when independent sets of characters—e.g., those obtained from the different life stages of chironomids—are used to produce classifications of species; to the extent that the resulting classifications agree, they are judged to be natural and real reflections of history. The same view can be applied at a higher level: To the extent that biological and geological area cladograms agree, they can also be regarded as real reflections of history.

THE FUTURE

What might be gained by pursuing the question of area cladograms and their generality? Will they change our view of the world? For the last century or so, biogeographers (or at least the zoologists among them) have had a rather uniform view of the world, represented by the six basic biogeographic regions: the Nearctic, Palaearctic, Oriental, Neotropical, Ethiopian, and Australian regions. This classical concept was developed by Sclater (1858) and Wallace (1876) on the basis of what was then known about the distributions of birds and mammals. As formulated by them, the regions correspond, for the most part, to modern continental geography: The Nearctic region, for example, is basically North America; the Neotropical, basically South America; and so on. The basis for this concept was not the interrelationships of smaller areas of endemism, however, but the distributions of widespread taxa shared among the smaller areas. Despite this possibly fundamental flaw, the arguments of Sclater and Wallace were, with few exceptions, convincing to other biogeographers over the years. Croizat was the notable exception in recent times, because he argued that biogeographic regions for terrestrial organisms correspond not to present continents, but to present ocean basins.

Current studies indicate that the oldest rocks surviving in the existing ocean basins date back only to the Jurassic, some 150 million years ago. According to the concepts of plate tectonics, if we start with the present configuration and put the time machine in reverse, the Atlantic

would become smaller and eventually disappear; India, and perhaps other lands bordering the Indian Ocean to the east, would come together in the western Indian Ocean with Madagascar; Australia would move southward and eventually attach to Antarctica; and the Pacific would become larger.

This concept resembles that of Sclater and Wallace in leaving to the continents, except India, past identities largely as we know them today. As the Pacific decreased in size, its old (pre-Jurassic) seafloor was subducted under the edges of the continents bordering its basin. The problem with this interpretation, however, is that the sea-floor spreading centers known today are all believed to have originated under continental masses (the Atlantic spreading center originating under Pangaea and later separating the Old and New World, etc.)—except for the spreading center now in the east Pacific. The east Pacific center, according to current views, was anomalous, appearing under and separating only the sea-floor.

Biogeographers have also found anomalies—in their case groups of organisms with trans-Pacific relationships. Croizat (1958), for example, argued strongly that past continental positions must have been different from the present ones, but was unable to accept classical continental drift theory simply because it could not explain trans-Pacific organismic relationships. Thorne (1973, p. 45) even went so far as to state that his view that South America houses as many (or more) plant groups with trans-Pacific relationships as it does groups with trans-Atlantic relationships appears "to rule out continental drift as a valid explanation for wide disjunctions in the ranges of seed plants"!

There have, however, been attempts to devise alternative geological models of the history of the Pacific region. Hughes (1975) considered North America west of the Rocky Mountains to have been part of Asia, rifted across a proto-Pacific ocean as the present Pacific was formed. Nur and Ben-Avraham (1977, 1978) hypothesized a Triassic Pacific continent, fragments of which are now found embedded around the rim of the Pacific basin. Shields (1979) presented a hypothesis, based on an expanding earth, of a Pacific completely closed by land in the early Jurassic.

If pieces of continents or island arcs have been rifted from what is now the mid-Pacific, sutured onto various continents, and carried organisms with them, then North America would contain organisms with Atlantic relationships and organisms with Pacific relationships. In that case, North America would not be an integral area biogeographically, but an amalgam of parts of two worlds, and the Nearctic and other classical regions would not be parts of the real world, but hybrids—artificial groupings of areas of endemism.

Biogeographers, then, can contribute to the resolution of a problem in earth history in a decisive way, and not be forced—as they have been in the past—merely to accept whatever geologists might tell them about earth history. They will have to conduct their own independent investigations into areas of endemism and their interrelationships, but all indications are that they can accomplish this task (Nelson and Rosen 1980).

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